

## Evolution of Human Growth Spurts

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**KEY WORDS** Subadult growth spurt, Anthropoid primates, Life history

**ABSTRACT** This study investigates subadult growth spurts in a large sample of anthropoid primates, including humans. Analyses of body mass growth curves show that humans are not unique in the expression of female and male body mass growth spurts. Subadult growth spurts are observed in both New World and Old World anthropoid primates and are more common in males than in females. Allometric analyses of growth spurts indicate that many aspects of primate growth spurts are strongly correlated with species size. Small species tend not to exhibit growth spurts. Although male and female scaling patterns for velocity and size measures are comparable, scaling relations of variables that measure the timing of growth spurts differ by sex. These patterns can be related to sexual differences in life histories. Scaling analyses further show that humans do not depart substantially from patterns that describe other anthropoid primates. Thus, in relative terms, human growth spurts are not exceptional compared to this sample of primates. The long absolute delay in the initiation of the human growth spurt may be of substantial evolutionary importance and serves to distinguish humans from other primates. In essence, humans exhibit growth spurts that are comparable to other primates in many respects. However, human growth spurts are shifted to very late absolute ages. © 1996 Wiley-Liss, Inc.

A controversial issue that has arisen from comparative studies of primate growth concerns the uniqueness of the human growth trajectory (Bogin, 1988, 1993; Gavan, 1982; Laird, 1967; Tanner, 1978; Tanner et al., 1990; Watts, 1985, 1986). Specifically, debate about the evolution of human growth often focuses on whether or not nonhuman primates show adolescent growth spurts in either length or mass. This problem is important because, as suggested by Bogin (1988, 1993), the human statural growth spurt may be a uniquely derived (autapomorphic) trait. He argues that this characteristic ranks with features such as bipedalism and large relative brain size in distinguishing humans from nonhuman primates (Bogin, 1993). This hypothesis implies that

considerable insight into the divergence of the human lineage may follow from the delineation of ecological and social correlates of growth spurts. Unfortunately, detailed comparative analyses of skeletal length growth in a broad sample of nonhuman primates are not currently possible. Researchers have presented evidence that conflicts with Bogin's statement, but there are potential problems with these studies.<sup>1</sup>

Although detailed analyses of length growth across primates are not possible, studies of mass growth can be undertaken. Unlike statural growth, Bogin (1988) finds that body mass growth spurts are occasion-

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Received July 31, 1995; accepted June 15, 1996.

ally present in anthropoid primates but probably only in males (1988). Specifically, he notes that female baboons, macaques, and chimpanzees lack a "visually detectable spurt in either linear dimensions or in weight" (Bogin, 1988:66). This observation implies that a female growth spurt in mass may be a uniquely derived human character. However, more recent analyses suggest that both females and males of some primate species exhibit visually detectable growth spurts in mass (Leigh and Shea, 1995; Leigh, 1995; Tanner et al., 1990), indicating a need for refinement of Bogin's assessment.

Debate about whether or not human growth spurts are uniquely derived is obviously important for gaining a better understanding of human evolution. However, questions about the evolution of growth spurts in mass have acquired additional significance as a consequence of recent advances in primate life history theory. Specifically, new theoretical analyses suggest that body mass growth rate variation is critical to the evolution of primate life histories (Janson and van Schaik, 1993; Sade, 1990). Growth rate variation can be linked to social and ecological factors that may explain why primates apparently have "slow" life histories compared to other mammals. Investigation of these links provides an opportunity to explain the evolution of human growth trajectories. Consequently, the present study explores growth rate variation in a

sample of 35 anthropoid primate species with the general objective of placing human growth into a comparative framework. More specific aims involve allometric analysis of primate growth as well as consideration of the adaptive and life history significance of body mass growth rate variation.

## MATERIALS AND METHODS

### Materials

The data analyzed consist of mixed-longitudinal chronological age and body weight measures for 2,395 captive primates representing 34 species (Table 1) and human data from the literature (Buckler, 1990). These animals are housed at zoological parks and primate centers throughout the world. Observations for each individual were obtained from records of routine veterinary examinations and tuberculosis tests. All measurements are from clinically normal animals, although some weight observations were collected from traumatized animals (provided the weight observation was collected soon after the incident of trauma). Additional details regarding the composition of this sample are reported elsewhere (Leigh, 1992a,b, 1994a,b; Leigh and Shea, 1995, 1996). Human weight growth data are taken directly from Buckler's study (1990) of adolescents in Leeds, England. This source provides extremely detailed information about adolescent growth in a number of morphometric variables. It should be recognized that body weight (as a measure of mass) is a tremendously important variable in evolutionary terms. As noted by Schmidt-Nielsen, (1984:9), "mass is of fundamental importance" in evolutionary biology. On the other hand, gain in body mass tracks growth in all somatic tissues, unlike statural growth, which records size increase mainly in bone and cartilage. Thus, a case can be made for analyzing mass growth interspecifically because body length covaries closely with locomotor behaviors (Jungers, 1984). Moreover, mass is closely tied to selection for metabolic efficiency and is used commonly in interspecific allometric studies.

### Methods

**Data analyzed.** All data are analyzed cross-sectionally, although longitudinal data

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<sup>1</sup>Bogin's contention contrasts with views advanced by the late Elizabeth Watts (1985, 1986; Watts and Gavan, 1982) and the late James Gavan (1982), who argued that nonhuman primates, represented by common chimpanzees (*Pan troglodytes*), exhibit a skeletal growth spurt (see also Tanner, 1978). This question has yet to be convincingly resolved. The data utilized by Watts and Gavan (1982) were collected many decades ago, and methods that are ideally suited to answering this question have only recently become available. New data and methodologies indicate that skeletal growth spurts may exist in nonhuman primates. Specifically, Tanner et al. (1990) find that female rhesus macaques (*Macaca mulatta*) seem to exhibit a pubertal growth spurt in linear dimensions. These data are from a sample of rather limited size (N = 15). On the other hand, Cheverud et al. (1992) fail to observe linear growth spurts based on cross-sectional growth data for wild toque macaques (*Macaca sinica*). Shea (1985) detects skeletal growth spurts in dentally aged cross-sectional samples of male and female gorillas. Information about the presence, phylogenetic distribution, and adaptive significance of linear growth spurts in known-age nonhuman primates is unavailable, precluding further investigation of this phenomenon.

TABLE 1. Species evaluated, sample sizes (individuals), presence or absence of growth spurt,<sup>1</sup> and female weight<sup>2</sup>

Species	Sample size (male/female)	Growth spurt (by sex)	Species size <sup>3</sup> (female weight, kg)
Ceboidea (New World monkeys)			
<i>Cebuella pygmaea</i>	36/51	None	.156
<i>Callithrix jacchus</i>	48/71	None	.352
<i>Callimico goeldi</i>	42/47	None	.621
<i>Saguinus fuscicollis</i>	18/19	None	.410
<i>Saguinus geoffroyi</i>	9/10	None	.493
<i>Saguinus imperator</i>	11/14	None	.525
<i>Saguinus oedipus</i>	46/18	None	.534
<i>Leontopithecus rosalia rosalia</i>	26/31	None	.659
<i>Saimiri sciureus</i>	32/28	None	.668
<i>Cebus apella</i>	26/28	Male	3.19
<i>Callicebus moloch</i>	30/23	None	1.241
<i>Aotus trivirgatus</i>	25/23	None	1.00
Cercopithecoidea (Old World monkeys)			
<i>Cercopithecus aethiops</i>	30/30	Both	3.453
<i>Cercopithecus mitis</i>	27/37	Male	5.593
<i>Cercopithecus neglectus</i>	29/23	Male	5.658
<i>Erythrocebus patas</i>	41/52	Both	6.691
<i>Cercocebus atys</i>	38/71	Male	7.823
<i>Macaca arctoides</i>	52/58	Male	12.150
<i>Macaca fascicularis</i>	13/13	Both	5.158
<i>Macaca fuscata</i>	64/71	Both	11.079
<i>Macaca mulatta</i>	52/58	Both	8.376
<i>Macaca nemestrina</i>	39/64	Both	7.502
<i>Macaca silenus</i>	39/41	Male	5.800
<i>Papio hamadryas</i>	33/53	Male	14.343
<i>Mandrillus sphinx</i>	49/59	Both	16.495
<i>Colobus guereza</i>	46/49	Both	9.259
<i>Presbytis entellus</i>	29/24	Both	13.497
<i>Presbytis obscura</i>	19/17	Male	6.402
Hominoidea (apes and humans)			
<i>Hylobates lar</i>	25/25	None	6.043
<i>Hylobates syndactylus</i>	19/21	None	11.362
<i>Pongo pygmaeus</i>	42/42	Male?	60.901
<i>Gorilla gorilla</i>	77/64	Both	80.864
<i>Pan paniscus</i>	13/23	Both	33.936
<i>Pan troglodytes</i>	22/23	Male	45.054
<i>Homo sapiens</i>	Literature data	Both	54.5 <sup>4</sup>

<sup>1</sup> Species with growth spurts are analyzed allometrically.<sup>2</sup> Text references to small species are those ranging from 100 g to 5 kg, medium-sized species are from 5.01 kg–20 kg, and large species are above 20.01 kg.<sup>3</sup> Data from Leigh (1994b).<sup>4</sup> Mean weight for an 18-year-old Leeds female from Buckler (1990: p. 259).

for each individual nonhuman primate have been visually inspected. Cross-sectional analysis precludes study of individual variation in growth spurts. In addition, Tanner (1978) has pointed out that cross-sectional treatment of human growth data leads to artificially depressed estimates of growth spurt magnitudes. This problem is evident in the current database for some species. However, artificial depression of growth spurts should lead to a conservative diagnosis of the presence of growth spurts. Consequently, it is unlikely that cross-sectional treatment of the data will show growth spurts that do not exist. In addition, the degree to which cross-sectional data distort

longitudinal growth representations depends on the level of variation in growth spurt timing within samples. In the present study, this difficulty is minimized because the species studied have short growth periods relative to humans. Shorter growth periods limit the time available for variance in growth spurts. For example, individual human peak velocities can be separated by several years, a time period that corresponds to the total length of the growth period in some of the nonhuman primates analyzed in this study. The short growth duration of many of the species in this study means that cross-sectional measures of growth spurts are probably less prone to error than comparable

estimates for humans. It should also be noted that cross-sectional results are consistent with longitudinal measures of growth (see Leigh, 1992a), although in cases where growth spurts are extreme, cross-sectional estimates do tend to underestimate growth spurt magnitudes.

**Smoothing techniques.** Nonparametric lowess regressions provide empirical descriptions of growth for each sex in each species (see Cleveland, 1979; Cleveland and Devlin, 1988; Efron and Tibshirani, 1991). Applications of lowess regression to this database have been detailed elsewhere (Leigh, 1992b, 1994a). Lowess regression involves choosing a smoothing parameter or tension ( $F$ ) that controls the rigidity of the predicted line, with an  $F$  of 1 resulting in a linear regression. Values closer to zero allow curvilinear fits to data. In all cases, lowess fits to data were visual inspected, and  $F$ -values were iteratively chosen until residual values from fits appeared to be normally distributed with a mean of zero. Typically,  $F$ -values between .3 and .5 returned the best fits for these data.

Lowess regression is quite flexible and does not impose an empirical structure on the data. In contrast, certain popular models of human growth include built-in growth spurt parameters (other parametric models may lack growth spurt parameters). Employing models that anticipate growth spurts may increase the likelihood of observing spurts. Lowess and related nonparametric models avoid this problem. Thus, nonparametric approaches are optimal for interspecific comparisons because the resulting descriptions of growth do not depend on a regression model's functional form. In addition, these models can serve as guides to choosing existing growth curves for subsequent studies of growth in certain species.

The relations between lowess fits and parametric models have been presented elsewhere. Specifically, Leigh and Shea (1996) modelled growth in African apes with a human growth model developed by Jolicoeur and colleagues (Jolicoeur et al., 1988). The Preece-Baines model has also been applied to data from African apes and compared to lowess fits (Leigh, unpublished).

The shapes of distance and velocity curves for both parametric and nonparametric curves are similar. However, the parametric models, because they are designed for humans, seem to force nonhuman primate subadult growth spurts to peak at late ages. Thus, while the use of nonparametric regressions may lack an extensive history, this approach seems to provide sufficient information for exploratory analyses of interspecific variation in growth.

Estimates of growth rates for nonparametric regressions are calculated by dividing the difference in successive predicted weight values ( $Y$ ) by the difference in successive age values ( $X$ ) (equivalent to Coelho's (1985) pseudovelocity curves). Pseudovelocity curves yield approximations of the first derivative for each sex in each species and are used to detect and measure growth spurts. Lowess curves fit clusters of cross-sectional data very tightly, resulting in jagged predicted curves in some cases. These changes of velocity are very subtle but are magnified upon calculation of pseudovelocities, particularly when observations were separated by irregular time intervals. Therefore, a second round of smoothing on the lowess-predicted values was undertaken in order to calculate pseudovelocities. The second round of smoothing was accomplished with spline regressions (Schluter, 1988). This technique proved robust to problems resulting from uneven age intervals between predicted values. This technique is thoroughly discussed by Schluter (1988) and by Cheverud et al. (1992). It involves a slightly more global fit to the data than does lowess regression. It should be noted that this second round of smoothing may have obscured some secondary changes in growth velocity (e.g., subtle spurts like the mid-childhood growth spurt in some humans). Consequently, the fits of curves at all stages during the smoothing process were carefully inspected. More specific information about the subtleties of growth in nonhuman (and human) primates must await the collection of ideal longitudinal data.

Subadult growth spurts are defined as unimodal, visually detectable increases in velocity that peak during the last two-thirds of the growth period. For nonhuman pri-

mates, these are termed subadult growth spurts because their endocrine correlates remain unknown, precluding their designation as adolescent growth spurts. In humans, adolescent growth spurts are defined as increases in velocity that peak between puberty and attainment of asymptotic size (Bogin, 1994). Whether or not the subadult growth spurts analyzed by the current study occur during a homologous developmental period is uncertain. Since the definition of a subadult growth spurt lacks a clear endocrine basis (cf. Metzger et al., 1994), I have presented pseudovelocity curves for thirty species, allowing readers to independently assess the attributes of subadult growth spurts. The terms *growth spurt* and *subadult growth spurt* are used interchangeably throughout the text.

**Allometric analyses.** Measurements of growth spurts include peak velocity, weight at peak velocity, age at peak velocity, takeoff velocity (defined as minimum prespurt growth rate), age at takeoff velocity, age at return to takeoff velocity, and duration of spurt (the difference in ages at takeoff and return to takeoff velocities (Fig. 1). These variables are analyzed in relation to sex and species size. Human growth data analyzed in the present study are summarized in Buckler's Table 8.1 (1990). These data include averages for peak velocity, age at peak velocity, weight at peak velocity, weight at 18 years of age (as a measure of adult size). Estimates of takeoff velocities, ages, and weights are obtained from Buckler's (1990) appendices and may not be fully congruent with estimates for other species in the sample. It should be recognized that there is obviously considerable variation in human growth (Bogin, 1988; Eveleth and Tanner, 1990). However, this variation probably does not override the interspecific variability that is the primary focus of the present analysis. The subtlety of female growth spurts for some species complicates measurements. For these cases, a fairly liberal definition of growth spurts is utilized.

Pseudovelocity curves are presented graphically for most species, using the Sygraph graphics package (Wilkinson et al., 1992). In addition, measurements of growth

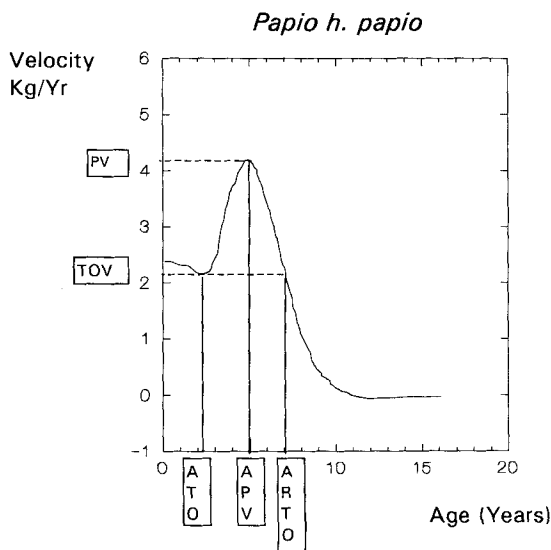


Fig. 1. Attributes of pseudovelocity curves measured in the present study. The X axis represents age (in years), and the Y axis presents pseudovelocity estimates (kilograms/year) for male red baboons. Dashed lines represent velocity measures: PV, peak velocity; TOV, takeoff velocity. Solid lines show measures of age: ATO, age at takeoff velocity; APV, age at peak velocity; ARTO, age at return to takeoff velocity. Growth spurt duration is measured by subtracting age at takeoff velocity from age at return to takeoff velocity. Measures of size are represented by average adult weight.

spurts are subjected to allometric analyses in order to understand their relations to size. This provides a direct way to evaluate the relationship of human growth to that of other primates with careful reference to size variation. In all cases, reduced major axis regressions are utilized to evaluate the relation between growth measures and size. These regressions account for error in both the dependent and independent variables (Sokal and Rohlf, 1981). All reduced major axis regressions are calculated in Systat's Nonlin module (Wilkinson et al., 1992). Humans are excluded from calculation of reduced major regression lines, but the X and Y coordinates of human measurements relative to the lines are plotted. This provides a measure of the degree of similarity between humans and other taxa without the influence of human data on the regression. Allometric results are presented mainly as plots (rather than as tables) because this ap-

proach preserves the relations among data points.

Evaluation of regressions between each independent variable and size is supplemented by phylogenetically adjusted correlations among variables. These adjustments follow procedures outlined by Garland and Adolf (1994), who recommend Felsenstein's (1985) method of independent contrasts. Branch lengths are calculated using information in Fleagle (1988), with updates where necessary. Correlations among independent contrasts are evaluated by regressions through the origin for each dependent variable and size. Large decreases in correlation values following calculation of independent contrasts suggests that regressions of raw (uncorrected) data may be biased by the lack of statistical independence among data points. It is assumed that the lack of a significant difference in adjusted and raw correlations allows use of uncorrected (raw) correlations for interpretations.

## RESULTS

### The phylogenetic distribution of growth spurts

Body mass growth spurts are not a universal feature of anthropoid primate ontogeny. However, subadult growth spurts are observed in certain species within each of the three anthropoid superfamilies (New World monkeys, Old World monkeys, and hominoids). Moreover, growth spurts occur in both female and male primates, with clearly defined spurts occurring more frequently in males than in females. New World monkeys do not generally exhibit growth spurts (sexes are combined in these plots because, with minor exceptions, female and male growth trajectories are similar) (Fig. 2). Most of these species tend to grow at a decelerating rate, producing smoothly declining pseudovelocity curves. Minor fluctuations are apparent at older ages, largely as a consequence of small samples. The small-bodied callitrichines generally do not grow for more than 2 years, regardless of adult body size (see Garber and Leigh, in press). Squirrel monkeys (*Saimiri sciureus*) resemble other small-bodied Neotropical primates in the shape of the pseudovelocity trajectory (Fig.

3). However, they exhibit sexual dimorphism in growth rates, with males growing slightly faster than females throughout the preadult period. Squirrel monkeys also grow for a relatively long period of time, ultimately producing a fairly high level of adult sexual dimorphism (Leigh, 1992a,b).

The only New World monkey in this sample with an unambiguous growth spurt is the black-capped capuchin (*Cebus apella*) (Fig. 3). Male growth velocity peaks at about 4.8 years of age at about 1.1 kg/year. Males may also show a growth acceleration at about 1.5 years of age. On the other hand, female capuchins do not exhibit a detectable growth spurt. But, unlike smaller Neotropical primates, they maintain growth velocities that are established early in life (about .5 kg/year) for nearly 2 years.

Growth spurts are a very common feature of ontogeny in Old World monkeys and are found in each of the two major cercopithecine tribes (cercopithecini and papionini) and in colobines. In cercopithecini, male growth spurts are highly variable in duration and magnitude and, to a lesser degree, in the timing of peak velocity (Fig. 4). Moreover, a clearly defined female growth spurt exists only in the patas monkey (*Erythrocebus patas*). Female vervet monkeys (*Cercopithecus aethiops*) also exhibit a growth spurt, but it is very slight. Female growth in blue monkeys (*Cercopithecus mitis*) and DeBrazza's guenon (*Cercopithecus neglectus*) lack growth spurts but show additional variation in patterns of growth rate deceleration. The growth rate of female blue monkeys declines in nearly linear fashion, while female DeBrazza's guenons present a stable, then steadily declining growth rate. Sex differences in growth rates at young ages are probably artifacts of small sample sizes. Similarly, initial velocities may not be accurately estimated because neonatal weight data are rare.

Variation in growth rates among macaques is substantial (Fig. 5). Males exhibit a growth spurt in all species examined. Females are more variable than males with respect to the presence of growth spurts. In addition, there are sex differences in the magnitude, duration, and timing of peak velocities in these species. The range in male

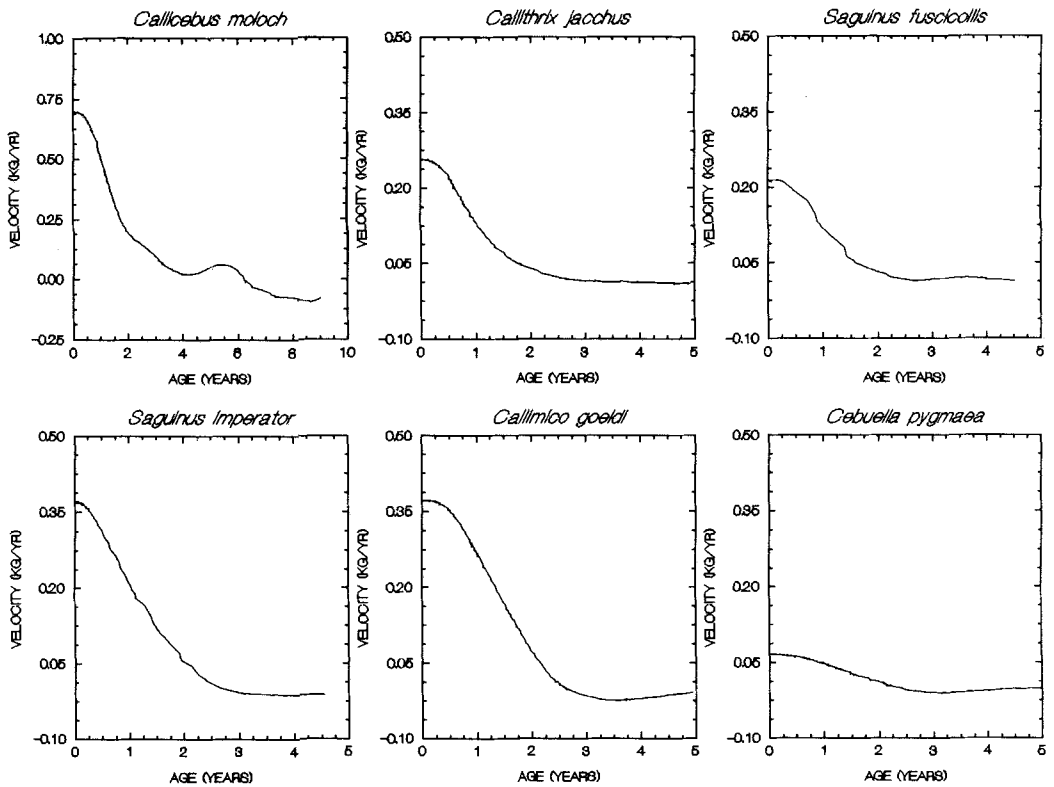


Fig. 2. Pseudovelocity curves for selected New World monkeys. Sexes are combined. All taxa are plotted to the same scale, except for *Callicebus moloch* (titi monkey). Not all species from Table 1 are shown, as growth trajectories are similar for smaller New World monkeys.

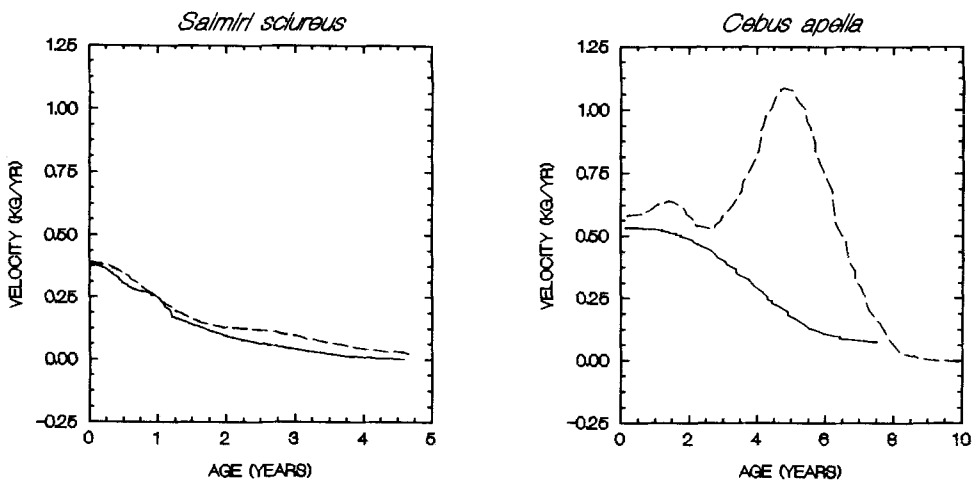


Fig. 3. Pseudovelocity curves for squirrel monkeys (*Saimiri sciureus*) and black-capped capuchins (*Cebus apella*). Note the sex differences (males are shown by dashed lines in this and subsequent plots).

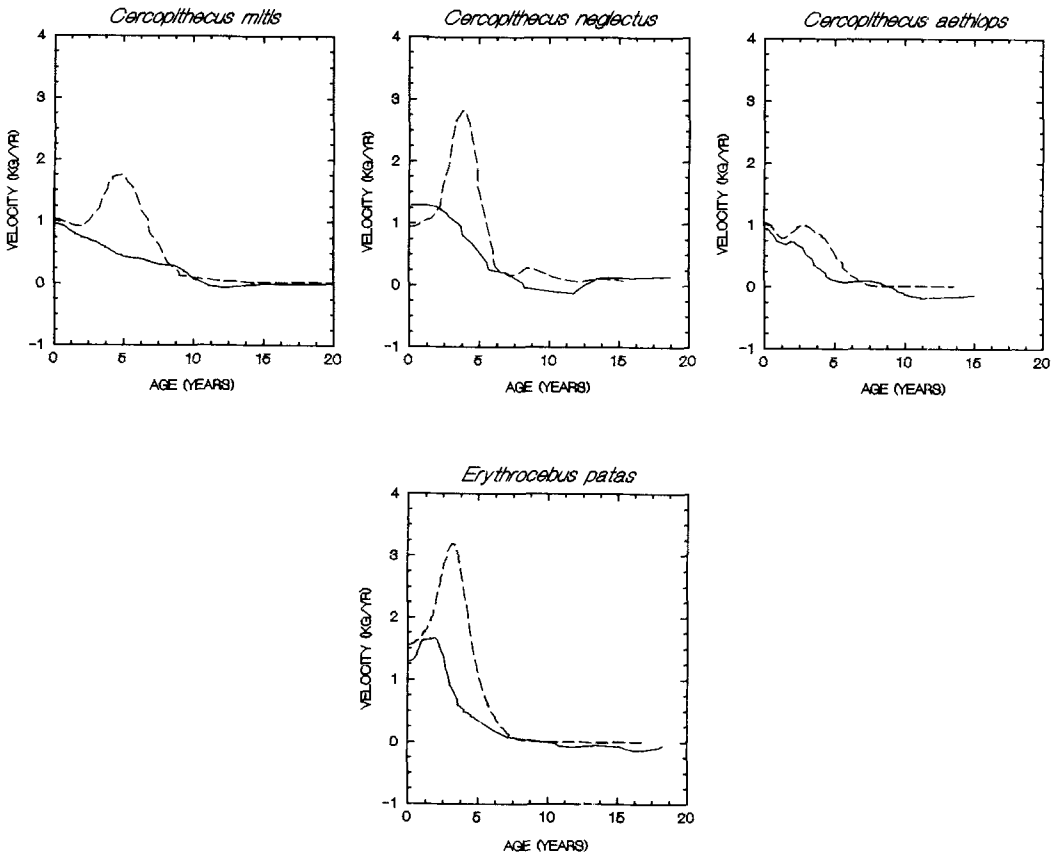


Fig. 4. Pseudovelocity curves for guenons. Species shown include *Cercopithecus mitis* (blue monkey), *Cercopithecus neglectus* (DeBrazza's guenon), *Cercopithecus aethiops* (vervet monkey), and *Erythrocebus patas* (patas monkey). Females are shown as solid lines; males are shown as dashed lines.

peak velocity extends from 3.72 kg/year in stump-tailed macaques (*Macaca arcoides*) to .97 kg/year in crab-eating macaques (*Macaca fascicularis*). Male macaques seem to have a secondary plateau in growth rates. Unfortunately, it is difficult to ascertain whether this is a consequence of small sample size or sample origin or a real phenomenon. Obvious female growth spurts are evident in rhesus (*Macaca mulatta*), pig-tailed (*Macaca nemestrina*), and Japanese (*Macaca fuscata*) macaques. Female growth spurts are poorly defined in lion-tailed (*Macaca silenus*) and crab-eating macaques. Female stump-tailed macaques (*Macaca arcoides*) apparently lack growth spurts.

Male red baboons (*Papio hamadryas papio*) and mandrills (*Mandrillus sphinx*)

are characterized by extremely high growth rates (Fig. 6). However, female papioninans generally show minimal growth spurts. The peak absolute magnitude of the male mandrill growth spurt exceeds that for all primates other than large-bodied hominoids. The timing and magnitude of growth spurts differ among colobines (Fig. 7). In addition, females in the two species evaluated exhibit well-defined growth spurts. Female growth spurts in these species are among the most obvious of all taxa studied.

Ape ontogeny varies considerably among species (Fig. 8). Growth spurts are absent in gibbons and siamangs. Growth in orangutans, particularly males, is unusual with respect to other primates. Mass growth for males appears to be indeterminate (unlike



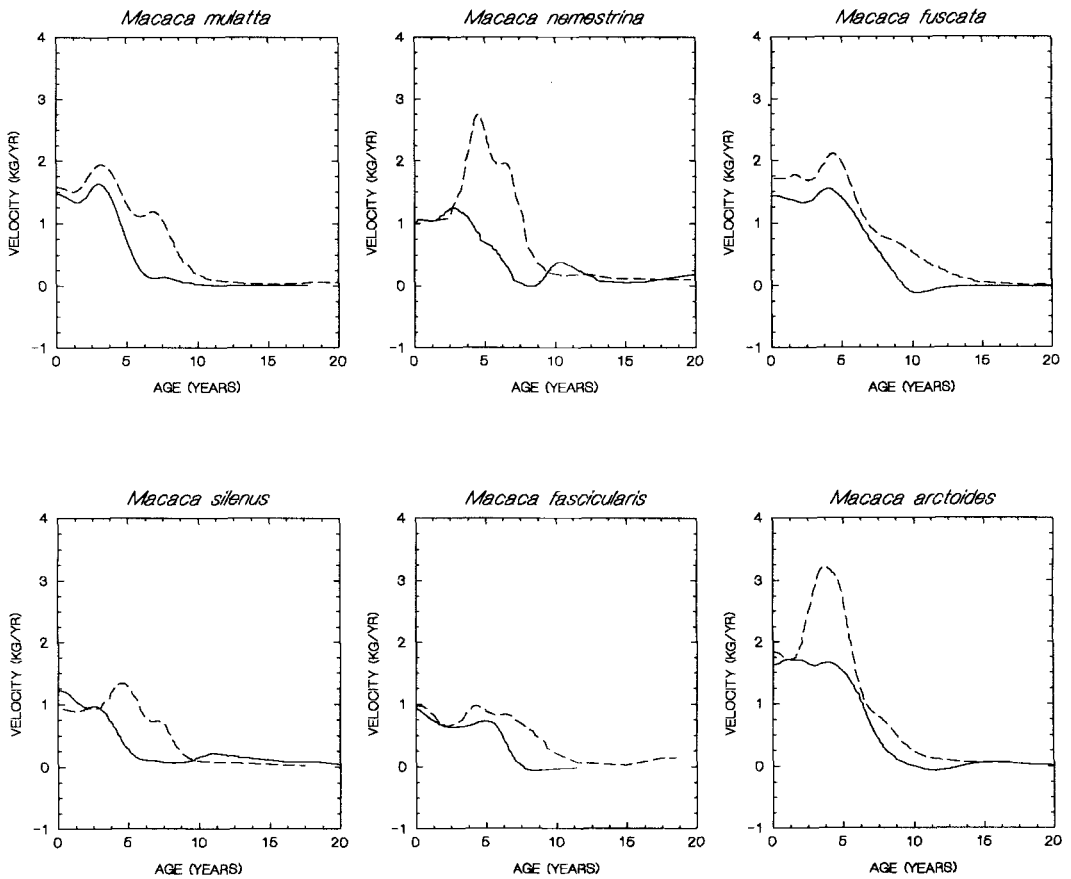


Fig. 5. Pseudovelocity curves for macaques. Species shown include *Macaca mulatta* (rhesus macaque), *Macaca nemestrina* (pig-tailed macaque), *Macaca fuscata* (Japanese macaque), *Macaca silenus* (lion-tailed macaque), *Macaca fascicularis* (crab-eating macaque), and *Macaca arctoides* (stump-tailed macaque). Females are shown as solid lines; males are shown as dashed lines.

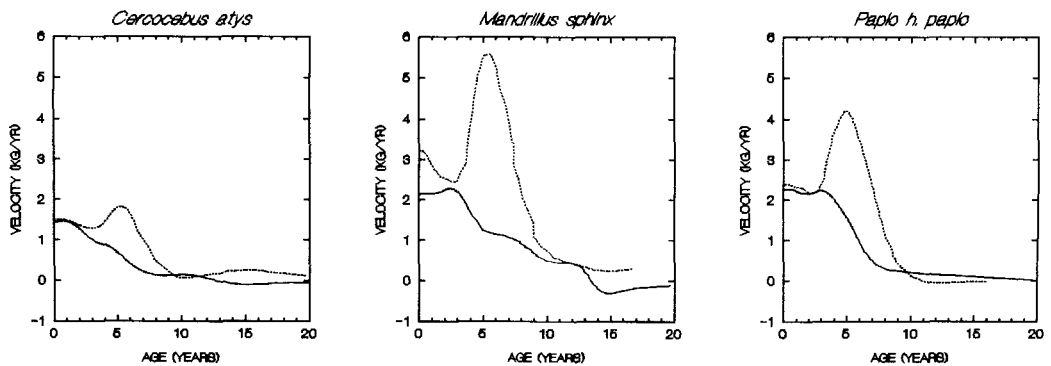


Fig. 6. Pseudovelocity curves for *Cercocebus atys* (sooty mangabey), *Mandrillus sphinx* (mandrill monkey), and *Papio hamadryas papio* (red or Guinea baboon). Females are shown as solid lines; males are shown as dashed lines.

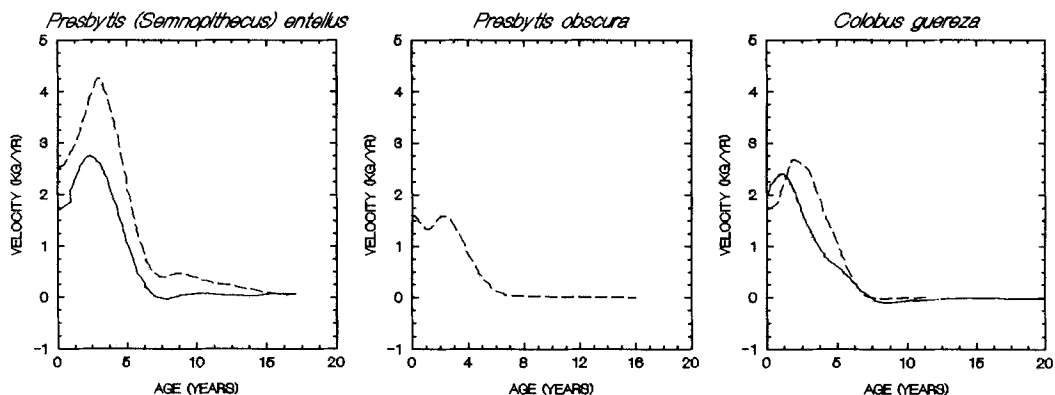


Fig. 7. Pseudovelocity curves for colobine monkeys. Species analyzed include *Presbytis (Semnopithecus) entellus* (Hanuman langur), *Presbytis obscura* (spectacled langur), and *Colobus guereza* (black-and-white colobus monkey). Data for female *Presbytis obscura* are not sufficient for the present analysis. Females are shown as solid lines; males are shown as dashed lines.

any other primate species), with a peak velocity reached at around 13.5 years of age. Orangutans are excluded from interspecific allometric analyses because of their unusual pattern of growth (for more detail see Leigh and Shea, 1995). Female orangutans seem to lack a single-peaked growth spurt that is comparable to other species. Growth spurts are apparent in the African apes (and in humans [Buckler, 1990]). However, female common chimpanzees, like orangutans, appear to lack a single well-defined growth spurt, in contrast to females of other African ape species (see Leigh and Shea, 1995, 1996). Female chimpanzees are considered to lack a growth spurt in this study. More complete comparisons of growth and development in apes are presented elsewhere (Leigh and Shea, 1995, 1996).

### Allometric analyses

Calculation of correlations between phylogenetically adjusted and raw variables suggests that phylogenetic relations among species do not artificially increase raw correlations. Specifically, *t*-tests indicate that average correlations do not differ significantly between phylogenetically adjusted and raw Pearson correlations ( $P = .921$  for females,  $P = .646$  for males). Consequently, a lack of statistical independence because of phylogenetic relations among species does not ap-

pear to influence the correlations between each measurement and species size.

The relationship between peak velocity and size is very consistent across this sample (Table 2). Moreover, expected values for male and female peak velocities are comparable at common sizes (Fig. 9). Humans (designated by ♀ and ♂ and excluded from the calculation of this and all subsequent regression lines) are only slightly below the female anthropoid regression line. Thus, humans are not extreme relative to other primates in terms of their peak velocities. For example, several macaque species and male common chimpanzees, like humans, have relatively low magnitude growth spurts. Relatively high magnitude growth spurts for both sexes are observed in both guenons and colobines. Comparison of weight at peak velocity relative to adult weight suggests that humans are large relative to other primates at peak velocity (Fig. 10). This may be related to the long duration of preadolescent human growth. Across primates and at any given size, males are expected to be slightly heavier than females at peak velocity. However, human females appear to be relatively heavier than male humans at peak velocity.

Humans reach peak velocity at absolute ages that are in excess of any other primate species (Fig. 11). Although humans are quite

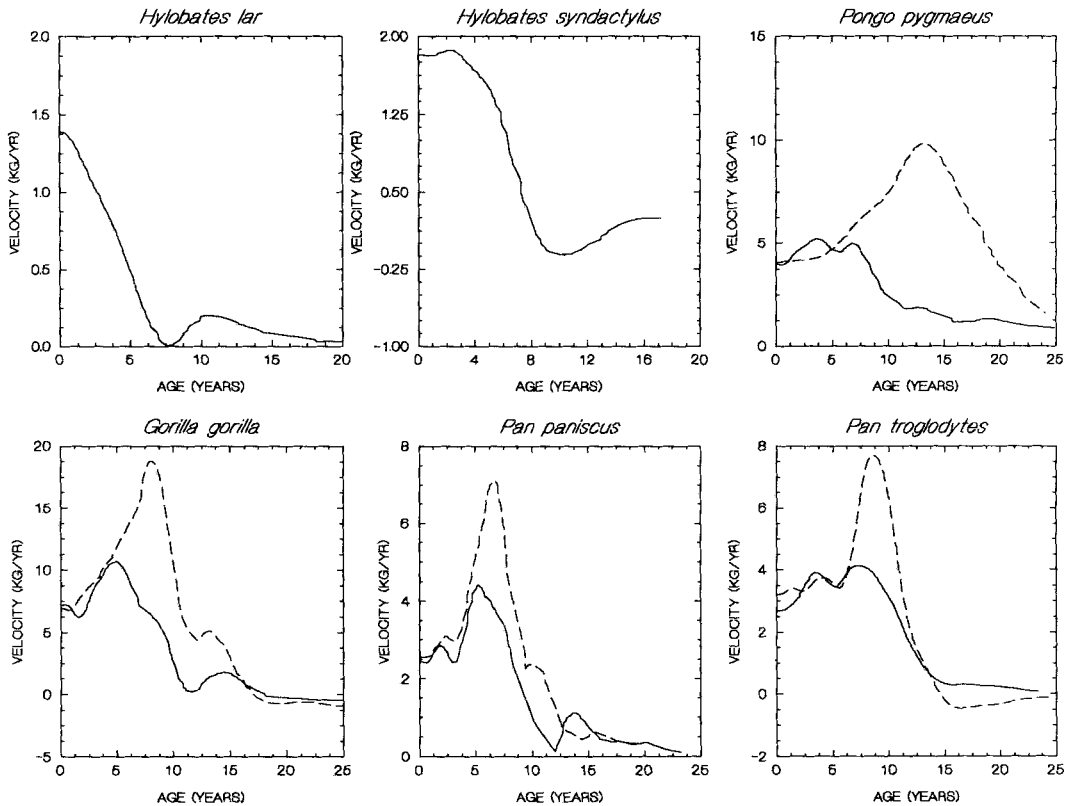


Fig. 8. Pseudovelocity curves for apes, including *Hylobates lar* (lar gibbon), *Hylobates syndactylus* (siamang), *Pongo pygmaeus* (orangutan), *Gorilla gorilla gorilla* (western lowland gorilla), *Pan paniscus* (pygmy chimpanzee), and *Pan troglodytes* ("common" chimpanzee). Females are shown as solid lines; males are shown as dashed lines.

TABLE 2. Reduced major axis regression results for analyses of growth spurt measures regressed against size (average male or female weight)<sup>1</sup>

Dependent variable	Intercept	Slope	Lower 95% CI on slope	Upper 95% CI on slope	Pearson correlation
Male peak velocity	-1.53	.92	.79	1.04	.97
Female peak velocity	-1.45	.87	.70	1.05	.97
Male weight at peak velocity	-.64	1.03	.94	1.11	.99
Female weight at peak velocity	-.64	.98	.78	1.17	.97
Male age at peak velocity	.15	.46	.28	.65	.72
Female age at peak velocity	-.37	.57	.16	.98	.63
Male growth spurt duration	.31	.41	.27	.55	.77
Female growth spurt duration	-.81	.70	.37	1.02	.76
Male takeoff velocity	-1.60	.73	.60	.87	.93
Female takeoff velocity	-1.30	.72	.54	.90	.94
Male age at return to takeoff velocity	.71	.40	.24	.55	.74
Female age at return to takeoff velocity	.11	.52	.22	.82	.76

<sup>1</sup> All regressions exclude human data points. Regression results for age at takeoff velocity are not presented because this variable is not correlated with size.

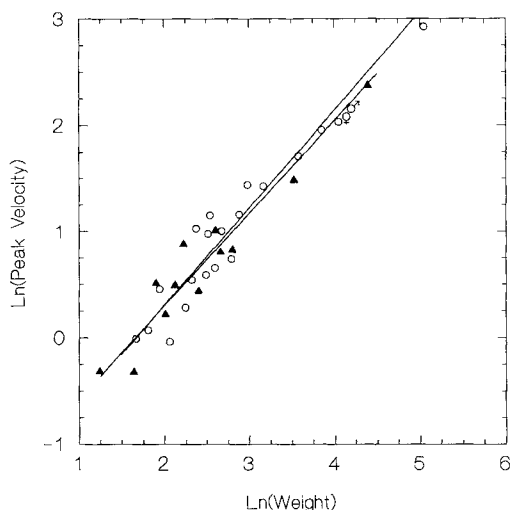


Fig. 9. Reduced major axis regression lines for peak velocity (kilograms/year) plotted against average adult weight (kilograms). Females are represented by triangles; males are shown by circles. Human females are identified by ♀; males are shown by ♂.

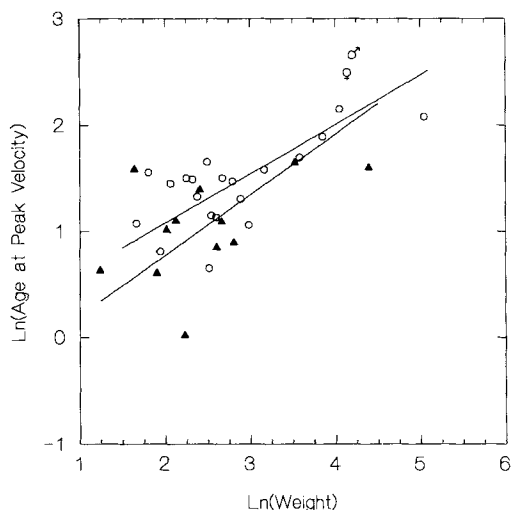


Fig. 11. Reduced major axis regression lines for age at peak velocity (years) plotted against average adult weight (kilograms). Females are represented by triangles; males are shown by circles. Human females are identified by ♀; males are shown by ♂.

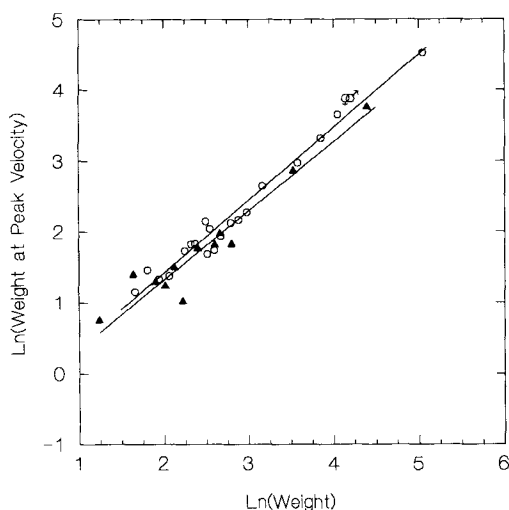


Fig. 10. Reduced major axis regression lines for weight at peak velocity (kilograms) plotted against average adult weight (kilograms). Females are represented by triangles; males are shown by circles. Human females are identified by ♀; males are shown by ♂.

distinct from an absolute standpoint, they are not atypical in relative terms. It is also important to note that there is considerable variation among primates in terms of both

absolute and relative age at peak velocity. The duration of the growth spurt, like many of the other variables analyzed, is positively correlated with size (Fig. 12). The human female growth spurt duration is relatively short. It should be noted that this could be a consequence of reliance on literature data. The duration of the human male growth spurt is also relatively quite short, but the departure from the regression line is less dramatic for males than for females. Across the remainder of the sample, anthropoid primates exhibit great variation in the duration of growth spurts across smaller size ranges (1.25–3 ln units of mass).

Age at takeoff velocity and size are not correlated, but humans exhibit very late ages at takeoff velocity (Fig. 13). However, takeoff velocity and size are closely correlated (Fig. 14). Thus, late age at takeoff velocity in humans is coupled with relatively low takeoff velocities, particularly in males. Across primates, female takeoff velocities are relatively higher than male takeoff velocities, as indicated by the difference in elevation between the female and male reduced major axis regression lines. Thus, at common sizes, female primates can be expected to have higher takeoff velocities than males.

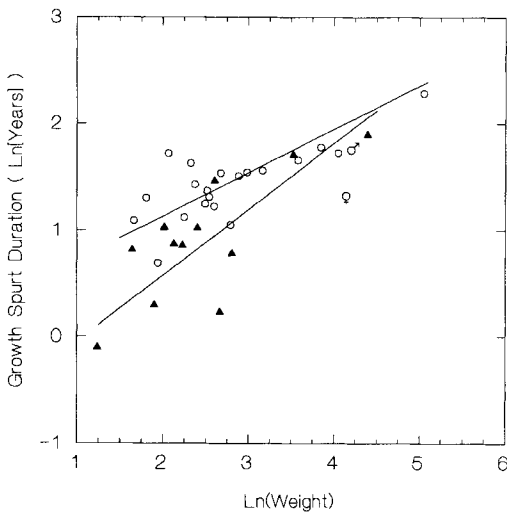


Fig. 12. Reduced major axis regression lines for growth spurt duration (years) plotted against average adult weight (kilograms). Females are represented by triangles; males are shown by circles. Human females are identified by ♀; males are shown by ♂.

This feature probably accentuates the male growth spurt because it helps produce a precipitous increase in growth rates. The human pattern, with the female takeoff velocity absolutely higher than the male takeoff velocity, fits the general primate pattern. Age at return to takeoff velocity and size are positively correlated (Fig. 15). In addition, the age at which males return to takeoff velocity can be expected to exceed female values at common sizes. Human ages at return to takeoff velocity are relatively and absolutely quite high (as could be expected based on the lateness of the human growth spurt).

Sexual dimorphism is present in some of the variables analyzed. Male primate growth spurts tend to exceed female growth spurts in duration, magnitude, and age of peak velocity. In addition, of the 21 species with male growth spurts (excluding *Pongo*), nine fail to show an unambiguous female growth spurt. The lack of a female growth spurt contributes considerably to adult sexual dimorphism. Neither male nor female peak velocity shows an association with sexual dimorphism (measured as the ratio of male to female adult weight). However, peak velocity dimorphism (male peak velocity divided by female peak velocity) is positively

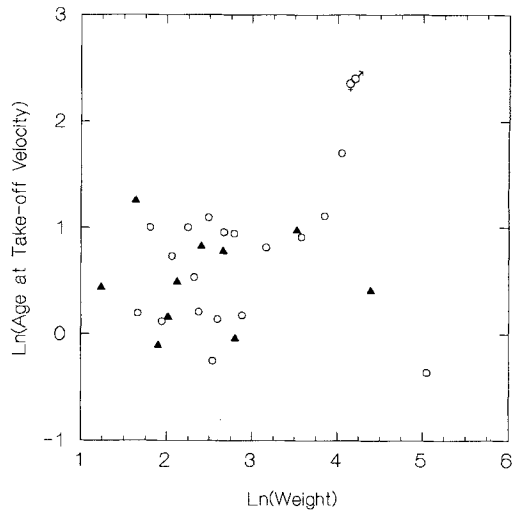


Fig. 13. Reduced major axis regression lines for age at takeoff velocity (years) plotted against average adult weight (kilograms). Females are represented by triangles; males are shown by circles. Human females are identified by ♀; males are shown by ♂. Note that humans have the latest ages at takeoff velocity. This variable appears to be independent of size.

associated with adult body size dimorphism ( $r = .874$ ). Dimorphism in both age at takeoff velocity and age at return to takeoff velocity are positively associated with adult body size dimorphism ( $r = .516$  and  $r = .680$ , respectively). Dimorphism in takeoff velocity and growth spurt duration appear to be independent of adult body size dimorphism. Humans are the least dimorphic species in the sample of primates with female growth spurts and show the least dimorphism in peak velocities. Mandrill monkeys exhibit the greatest dimorphism in peak velocity.

## DISCUSSION

### Growth spurts in a comparative perspective

This research shows that there is considerable diversity in subadult growth spurts for body weight in anthropoid primates. At least two basic kinds of variation in growth spurts are apparent. First, growth spurts are present in some species but not in others. Second, when growth spurts are observed, they vary considerably, both absolutely and relatively in age at initiation, magnitude, duration,

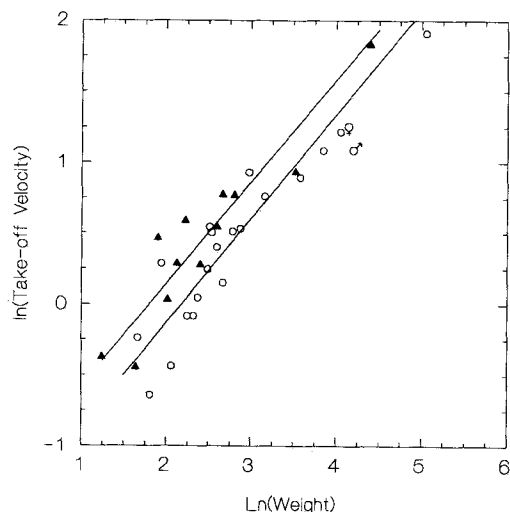


Fig. 14. Reduced major axis regression lines for take-off velocity (kilograms/year) plotted against average adult weight (kilograms). Females are represented by triangles; males are shown by circles. Human females are identified by ♀; males are shown by ♂.

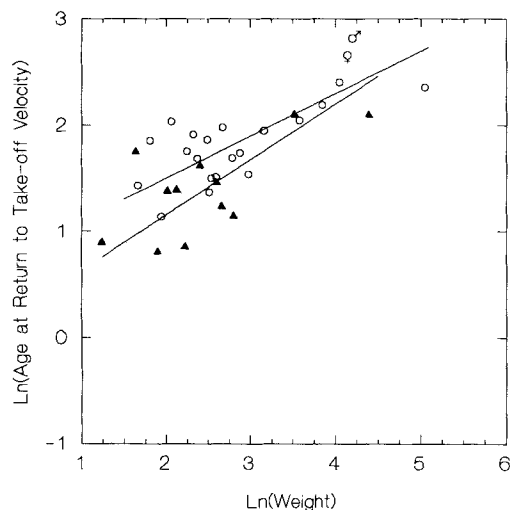


Fig. 15. Reduced major axis regression lines for age at return to takeoff (years) velocity plotted against average adult weight (kilograms). Females are represented by triangles; males are shown by circles. Human females are identified by ♀; males are shown by ♂.

timing of peak velocity, and age at cessation. Males are more likely than females to exhibit growth spurts, and most measures of growth spurts are correlated with size.

Variability in the presence of growth spurts across primates allows clarification of previous views regarding the phylogenetic distribution of growth spurts. As recognized by Bogin (1988, 1993), growth spurts are by no means a universal feature of primate growth and development. However, the present study finds that growth spurts in mass are fairly common among anthropoid primates. In addition, female growth spurts are more widespread than may have been previously realized. Thus, human females are unique neither in the expression of a mass growth spurt (see also Leigh and Shea, 1995, 1996) nor apparently in the possession of a skeletal growth spurt (Shea, 1985; Tanner et al., 1990).

The presence of a growth spurt in each of the three anthropoid superfamilies (New World monkeys, Old World monkeys, and hominoids) may suggest that growth spurts have evolved independently (or have been lost independently) in several lineages. Specifically, the lack of growth spurts in most platyrrhines coupled with the presence of a growth spurt in *Cebus* may suggest that the primitive platyrrhine lacked a growth spurt. This is, however, a tentative assessment because of the small sample of New World genera examined. Growth spurts are quite common among catarrhines, but the phylogenetic history of this character is even more difficult to resolve. The wide distribution of subadult growth spurts in catarrhines may suggest that this feature has evolved (or has been lost) independently in several lineages.

The presence of anthropoid primate growth spurts may be partly size-related. Specifically, small-bodied New World monkeys lack growth spurts and show a continuously decelerating growth rate. The growth spurts of smaller species within catarrhines are either weakly defined or absent (e.g., vervets within the Cercopithecoidea; gibbons and siamangs among apes). Data for talapoin (*Miopithecus talapoin*), the smallest Old World monkeys, are not adequate for this analysis. However, visual inspection of limited growth data suggests that they lack growth spurts (Leigh, 1992a). In contrast, weights at peak velocity, ages at peak velocity, growth spurt duration, takeoff velocities, and age at return to takeoff velocity are char-

acteristically high in medium-sized to large species ( $>10$  kg). Only age at takeoff velocity appears to be size-independent. Thus, growth spurts contribute to size differences among primate species along with differences in growth duration. Although growth spurts are correlated with size differences across primates, residual variation around the allometric regression lines exists for all variables. Residual variation for estimates of growth spurt timing is substantial. These variables show smaller correlations with size than do measures either of velocities or sizes at certain points in time. It can be noted that the small size of the earliest anthropoids (Simons and Rasmussen, 1994) may imply that these taxa lacked growth spurts.

The adaptive significance of variation in subadult growth spurts is difficult to gauge because the available behavioral and ecological data for most of these species are limited. However, recent theoretical considerations provide some understanding of this variation. Specifically, Janson and van Schaik (1993) identify two interrelated factors that may influence primate growth rate evolution. They suggest that, when risks of predation are high, natural selection favors group formation. However, group formation increases intraspecific feeding competition. This kind of competition probably affects juveniles more severely than other group members because young animals lack the foraging skills of larger, more experienced animals. Juveniles are also attractive to predators, which forces juveniles to forage at the center of groups, where feeding competition is likely the most severe. Under such conditions, natural selection against high growth rates can be expected because high growth rates result in high metabolic costs. Juveniles can avert the metabolic risks that intraspecific feeding competition entails by growing slowly while avoiding predation by foraging in a group.

Sufficient data for detailed analyses of the relations between predation, intraspecific competition, and growth spurts across primates are unavailable (but see Leigh and Shea, 1995, 1996). However, it can be suggested that subadult growth spurts may reflect periods along a developmental trajec-

tory when metabolic risks are concentrated. The tendency of growth spurts to occur at later periods during growth may imply that evolution has produced a tendency for incurring such risks later, rather than earlier, in life. Moreover, correlations with size may suggest that incurring risk during late periods of growth is a necessary trade-off for reaching adult size. Variation in the magnitude, duration, and timing of growth spurts among species and between sexes may reflect evolutionary diversity in the ways in which anthropoid primates counter or offset metabolic risks.

The assumption that metabolic risks are elevated by growth spurts implies that female primates may confront generally lower metabolic risks than do males, particularly in those species that lack female growth spurts. Although relative peak velocities (and implied relative risks) are comparable for each sex, the duration of the female growth spurt is relatively shorter than the male growth spurt. This reduces the time interval of risk, even though peak relative risks are about the same for each sex. On the other hand, females may face higher risks than males at the initiation of the growth spurt, as shown by their relatively higher takeoff velocities. Females also reach peak velocity somewhat earlier than males. These sex differences indicate that alternative female and male strategies of metabolic risk aversion have evolved in primates. Females displace metabolic risks to time periods that are, compared to males, relatively early in life. This pattern is expected because the chances of pregnancy increase with age. Females that support both a growth spurt and a pregnancy, followed by an infant, would incur very high metabolic risks. Thus, natural selection may have favored high female takeoff velocities at the expense of prolonged growth spurts that peak late in the preadult period. Longer and later female growth spurts would result in conflicts between the metabolic requirements of growth and those of reproduction. This explanation is consistent with analyses of human growth. Scholl and colleagues (Scholl et al., 1994, 1995) indicate that maternal-fetal competition, particularly for micronutrients, may be responsible for low birth weight in

adolescent mothers. Similarly, Frisancho et al. (1985) found that infants born to females who are still growing tend to have low birth weights. It should be noted that human female growth spurts are exceptionally short, with only one nonhuman species exhibiting a relatively shorter growth spurt.

Male peak velocities occur, with the exception of crab-eating macaques (*Macaca fascicularis*), at later ages than female peak velocities. One reason for this general pattern is that male growth is not influenced by the metabolic risks of pregnancy. In addition, retaining a juvenile size and shape for a long time relative to females may reduce the chances for intermale competition (Jarman, 1983; Leigh, 1995). In effect, males in species characterized by reproductive competition may face a trade-off between early and later reproductive opportunities by maintaining a juvenilized morphology as long as possible. This may be an available strategy because male growth spurts are not constrained by the metabolic risks of pregnancy. Bogen offers a parallel explanation for differences in the timing of human female and male statural growth spurts (1993). He suggests that sex differences in human sexual and social roles favor growth spurt timing differences. Social factors may have favored males that defer growth spurts (and thus attainment of final adult size) until as late as possible. This may explain why sexual dimorphism in adult size is related to sex differences in growth spurt magnitude and duration. Although sexual dimorphism can be produced in the absence of growth spurts (with *Saimiri sciureus* (squirrel monkey) providing an excellent example), male growth spurts tend to be found in sexually dimorphic taxa. Moreover, differential expression of male growth spurts across primates is related to factors involving species-specific social and life history adaptations (Leigh, 1995).

Social correlates of growth spurts are coupled with dietary influences on ontogeny. For instance, growth spurts covary with dietary differences among anthropoid primate species. Folivory and high protein intake are associated with elevated growth rates in primates (Leigh, 1994a), suggesting a major dietary influence on the evolution of body mass growth curves. Growth spurts in colobine

primates reflect a relationship between folivory and high growth rates. This association is especially obvious in female colobines (represented here by *Colobus guereza* (black-and-white colobus) and *Presbytis entellus* [Hanuman langurs]). Both species have relatively high peak velocities, and female colobus monkeys are exceptionally young at both the initiation of the growth spurt and at peak velocity. Female patas monkeys (*Erythrocebus patas*) also show a pronounced growth spurt, and this may be related to high levels of dietary protein through faunivory (see Leigh, 1994a). Males of these taxa (as well as *Presbytis obscura* [spectacled langurs]) also reach peak velocities relatively early in life. Dietary correlates of high growth rates have been discussed previously and apply to the present findings (see Leigh, 1994a).

### Human growth

The results of this study imply that the human growth spurt in mass is unusual in some respects. Specifically, variables that relate to the timing of human growth spurts are distinctive in relation to other primates. Human distinctness in certain timing variables is a consequence of the well-known prolongation of human growth. According to Laird (1967), the extremely long period of human growth results from the "insertion" of an interval of growth between infancy and adolescence. The present analysis shows that one consequence of this insertion is a growth spurt that is unlike those of most other primates with respect to timing variables (age at takeoff velocity, age at peak velocity, and age at return to takeoff velocity). Scaling analyses demonstrate that this delay is somewhat greater than would be expected relative to size based on other anthropoid species. However, several other species exhibit comparably long relative delays, suggesting that humans are not unique in this aspect of their growth spurt. In addition, human growth spurts are unremarkable with respect to other variables. Specifically, humans do not appear to be aberrant relative to other primates in both absolute and relative measures for peak velocity, size at peak velocity, and takeoff velocity. The duration of the growth spurt in human females seems short compared to other pri-



mates but does not necessarily represent an extreme (especially when the difficulties in measuring this variable are considered). The scaling perspective of this study also suggests that previous ideas about the uniqueness of human growth may have been influenced by the lack of an adequate comparative sample. For example, rhesus macaques have traditionally been used in comparative studies of primate growth (Laird, 1967; Watts, 1986). However, this species exhibits a growth spurt that is early relative to adult size, possibly exaggerating the interpolated differences between human and nonhuman primates with respect to growth spurt timing. Moreover, the absence or ambiguity of a female growth spurt in common chimpanzees (the other species historically used in comparative studies) may have highlighted some of the exceptional aspects of human growth.

The distinctive absolute delay of the human growth spurt may reflect a pattern of risk distribution for humans that is unusual compared to other primates. Specifically, the risks associated with growth spurts have been greatly deferred in humans. More specific correlates of the delay in human growth spurts are difficult to define. Assuming that Janson and van Schaik's (1993) model holds for humans, the period of childhood may be a period of fairly high risk, which has resulted in the evolution of depressed growth rates. The delay in the human growth spurt, like that of many other primates, may involve life history trade-offs between slow childhood growth and body size requirements for reproductive adults. The trade-off towards prolonging childhood seems particularly extreme and requires additional analysis. In essence, the human growth spurt, which is otherwise consistent with size-adjusted primate standards, is shifted to late ages. This may suggest that the evolutionary forces that have acted on later human growth (during the ages covering the growth spurt) are not all that unique relative to nonhuman primates.

Analysis of human growth suggests that several alternatives and modifications to Janson and van Schaik's (1993) model can be considered. First, brain growth may play a role in deferring the human growth spurt.

Specifically, body mass growth spurts in humans may be deferred until growth of the absolutely and relatively large human brain (with its high metabolic costs [Lehninger, 1982]) is complete. However, human brain growth may cease as early as 6.01 postnatal years in males and 6.40 postnatal years in females (Jolicoeur et al., 1988). Thus, brain growth ceases at least 4 years before human takeoff velocity as measured in the present study. Interestingly, female human brain growth occurs absolutely slower over a longer period of time than male brain growth. Although there is debate about the precise age of brain weight growth cessation (see Jolicoeur et al., 1988) metabolic competition between brain and body weight growth would not seem to explain the difference between brain growth cessation and growth spurt initiation. However, the difference in the timing of these events might indicate that investigation of the period from 6–10 years of age is critical to explaining the evolutionary origins of the additional period of human growth.

A potentially attractive and related alternative is that the period between brain growth cessation and adulthood is necessary for learned behaviors. This idea does not necessarily preclude Janson and van Schaik's (1993) model and has been frequently discussed (see Bogin, 1988; Poirier, 1977; Tanner, 1978). Furthermore, learned cultural behaviors are obviously much more important to humans than to other primates (Bogin, 1993). It is possible that certain critical components of language are acquired in the time interval between brain growth cessation and the commencement of somatic growth spurts. Again, this may suggest that understanding the evolution of human (and nonhuman primate) development lies in understanding the interval between brain growth cessation and either growth spurt initiation or adulthood. Unfortunately, almost nothing is known about brain growth duration in more than a few nonhuman primate species.

Explanations that involve learning and social experience do not necessarily conflict with a risk model. For example, Bogin (1993) notes that sex differences in social perception may have played a role in the evolution

of sex differences in human growth spurts. Some of these processes may not differ qualitatively from social processes in other primates. While the present analysis does not resolve these issues, it points to other primates that may be productive as analogs for studying the relations between the evolution of human behavior and somatic ontogeny. Moreover, intensive investigation of behavioral and ecological aspects of the period between birth and the initiation of the subadult growth spurt across primates, including humans, is required. At the most basic level, the present analysis finds that humans are not unusual in terms of body mass growth spurts *per se*. However, the long absolute delay in arriving at a growth spurt may signal either the importance of cultural factors (Bogin, 1988, 1993), a uniquely human profile of risks, or both.

### CONCLUSIONS

This comparative analysis demonstrates variation in the presence and attributes of body mass growth spurts in primates. Measures of growth spurts across a sample of nonhuman primates indicates that, when growth spurts are present, they vary in the timing and size at initiation, peak velocity and timing of peak velocity, and in duration. Growth spurts are more common in males than in females. Most measures of growth spurts are related to size, although residual variation is quite substantial in some cases.

In general terms, humans are not unique with respect to body mass growth spurts. The timing of growth spurts is the most distinctive aspect of human growth. However, variables that measure the timing of growth spurt events are not extraordinary once body size is considered. Measurements of velocities and duration are consistent with expectations based on size.

Variability in growth spurts across primates, including humans, may be related to differential patterns of ecological risk aversion. Sex differences in growth spurts may reflect sex differences in life history strategies and in risk aversion. Consideration of human growth suggests that acquisition of social skills and other learned behaviors may be important in the evolution of human

growth. The large comparative sample analyzed in this study provides a necessary foundation for approaching these alternative explanations.

### ACKNOWLEDGMENTS

This research was aided by the dedicated veterinary, curatorial, and animal care staffs at the institutions from which data were collected. I thank these individuals and institutions, including Dr. Anne Baker (Brookfield Zoo); Drs. Tom Meehan and Jim Letcher and Ms. Pat Sass (Linclon Park Zoo); Dr. Andy Teare and Mr. Jan Rafert (Milwaukee County Zoo); Ms. Ingrid Portan (St. Louis Zoo); Dr. Amy Shima and Ms. Kay Munduate (San Diego Zoo and San Diego Wild Animal Park); Dr. Doug Armstrong and Ms. Sarah Junior (Henry Doorly Zoo, Omaha); Dr. Tim Reichard (Toledo Zoo); Dr. Albert Lewandowski (Cleveland Zoo); Drs. Richard Cambre and Dave Kenney (Denver Zoo); Dr. Mike Burton (Cheyenne Mountain Zoo, Colorado Springs, CO); Drs. Paul Calle, Danny Wharton, Fred Koontz, and Robert Cook (Bronx Zoo); Dr. Lynne Kramer (Columbus Zoo); Dr. Mark Campbell (Cincinnati Zoo); Dr. Julian Duvall (Indianapolis Zoo); Drs. Debra Forthman, Beth Stevens, and Rita Macmanamon and Ms. Cindy Thorstad (Atlanta Zoo); Dr. Roy Burns (Louisville Zoo); Drs. Mark Peckham and Joe Flanagan and Ms. Barbara Lester (Houston Zoo); Ms. Donna Todd and Dr. Rodney Walker (Jackson Zoo); Drs. Mark Stetter and Susan Wells (Audubon Park Zoo, New Orleans); Mr. Jake Yelverton (Louisiana Purchase Gardens and Zoo, Monroe, LA); Ms. Linda Sanders (Baton Rouge Zoo); Mr. Will Sugge and Drs. Edwin Gould and Benjamin Beck (National Zoological Park); Drs. Ben Gonzales and Gary Kuehn and Mr. Victor Bolanos (Los Angeles Zoo); Dr. Les Shobert (North Carolina Zoo); Ms. Greta Macmillan (Knoxville Zoo); Mr. Donald Moore (Syracuse Zoo); Drs. Jim Else, Harold McClure, and Jeremy Dahl and Ms. Sue Setzekorn (Yerkes Regional Primate Research Center and grant number RR00165); Dr. Freeland Dunker, Ms. Gail Hedberg, and Dr. Myron Sulak (San Francisco Zoo); Mr. Robert Evans (San Antonio Zoo); Dr. James Kirkwood (London Zoo); Mr. F.M. Lockyear

and Mr. Peter Halliday (Port Lympne and Howletts Zoo Parks); Dr. Laurence Gledhill (Woodland Park Zoo); and Dr. Nate Flessness (International Species Information System). Drs. Jill Bullington, Barry Bogin, and Emöke Szathmáry provided helpful comments on an earlier version of the manuscript, as did an anonymous reviewer. Financial support for this research was provided by Northwestern University, Sigma Xi, the Wenner-Gren Foundation, and National Science Foundation grant number DBS9225084.

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